Meridional variations in the concentration of chlorophyll and microparticles in the North Pacific Ocean

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Abstract—The vertical distributions of chlorophyll *a* and microparticle concentration were recorded along two meridional transects of the eastern Pacific Ocean. One transect, obtained during the winter along 150°W, covered 15°S to 15°N, and the other transect, obtained during the summer along 155°W, covered 23°N to 57°N. Both distributions were measured optically: Chl *a* concentration was determined from the *in situ* fluorescence of Chl *a*, and microparticle concentration was determined from the transmittance of a collimated beam of light at 665 m.

Two patterns are apparent from the data. First, meridional changes in the concentration of Chl *a* are paralleled by changes in particle concentration. Chlorophyll concentrations are high at the equator and at high latitudes where the concentrations of microparticles are also high. An examination of the vertical distributions of water density and nitrate concentration suggests that this pattern appears to be determined largely by the concentration or rate of supply of nitrate to the euphotic zone.

Second, for a given latitude the vertical distribution of Chl *a* is predominantly caused by increases in the mean concentration of pigment within the microparticles. The ratio of Chl *a* to particle concentration is lowest in the surface layer. It increases rapidly below the surface layer, and it reaches a maximum value at or just below the depth of the chlorophyll maximum. Below the chlorophyll maximum, the ratio decreases slowly with depth. These changes appear to be a result of photoadaptation by phytoplankton and are consistent with recent mathematical descriptions of this process derived from studies of laboratory cultures.

INTRODUCTION

WHILE the general ecological factors that determine the concentration and distribution of phytoplankton in the sea are well known, detailed explanations for patterns of spatial and temporal distributions are still lacking. Patterns of distribution are determined by turbulent and advective transport, by factors such as light intensity, nutrient concentration, and temperature that affect the growth rate of phytoplankton, and by factors such as sinking and grazing that affect the rate of loss of phytoplankton.

Unfortunately, in many geographical regions oceanographers are unsure of the relative importance of these factors. A good example of such uncertainty is the diverse explanations proposed for the formation of the deep chlorophyll maximum commonly found in the open ocean. It has been proposed that this feature originates from the accumulation of cells sinking from surface waters (STEELE and YENTSCH, 1960), from increases in cell concentration caused by either increased rates of growth or decreased

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rates of loss from grazing (e.g. ANDERSON, 1969; VENRICK *et al.*, 1973; CULLEN, 1982), or simply from changes in cellular pigment concentration caused by photoadaptation (EPPLEY *et al.*, 1973; KIEFER *et al.*, 1976).

In an attempt to understand better the distribution of phytoplankton and chlorophyll in the open ocean, we conducted a survey of optical and hydrographic properties of the upper water column in the central north Pacific Ocean. The survey, which included waters between 15°S and 57°N, consisted of continuous vertical profiles of Chl *a* fluorescence, the beam attenuation coefficient, irradiance, temperature and salinity as well as discrete measurements of inorganic plant nutrients, Chl *a* concentration, and microparticle concentration. It is well known that *in situ* fluorometers can give an accurate measure of Chl *a* concentration provided there is sufficient calibration with discrete measurements of extracted pigment concentration. Less well known is the fact that profiles of the value of the beam attenuation coefficient at 665 nm obtained with transmissometer provide continuous information on the concentration of microparticles. In the open ocean these particles are predominantly microorganisms and associated detrital material smaller than 20 μm in diameter.

Like earlier studies of fluorescence and beam transmission (KIEFER and AUSTIN, 1974; LIEBERMAN *et al.*, 1984), we have found that simultaneous measurements of fluorescence and beam attenuation provide two distinct parameters of phytoplankton distribution. Unlike these earlier studies where sampling was limited to coastal waters of the temperate Pacific, we present results from an open oceanic area covering an extremely large geographic range. Moreover, we attempt for the first time to explain the patterns observed in chlorophyll and particle concentration in terms of the i..teracting effects of nutrients, light, and vertical mixing upon the growth and metabolic regulation of the phytoplankton and cyanobacterial plankton crop.

METHODS

Some optical and biological measurements combined with CTD casts were made during two cruises on R.V. *Discoverer*: 27 February–9 March, 1984 along 150°W longitude between 15°N and 15°S, and 28 June–23 July, 1985 along approximately 155°W longitude between 23°N and 57°N. Additional data were taken during the ODEX-3 cruise, 10 October–17 November, 1982 in the area of approximately 220×220 km^2 centered at 33°N, 142°W.

The Oregon State University k-meter package consists of a Biospherical Instruments Spectroradiometer, a CDT using Seabird sensors, a Q Instruments *in situ* fluorometer, and a transmissometer with 25-cm pathlength developed by Oregon State University (BARTZ *et al.*, 1978). Water samples were taken by a separate cast at each station for chlorophyll, nutrient and particle size analyses.

An opal glass spherical collector was placed over the cosine collector of the spectro-radiometer to convert it from a vector to a scalar irradiance meter. In order to compensate for changes in incident radiation during casts, we monitored irradiance on deck using a Biospherical Instruments Solar Reference Hemispherical irradance sensor which measures the total photosynthetically active radiation. The collector has a shroud to block light from below the horizontal plane and is gimbal-mounted at the top of an A-frame away from any shadows.

With the transmissometer we obtain the transmission (I/I_o) of a collimated beam of monochromatic (665 nm) light. From this, the beam attenuation ($c = -\ln(I/I_o)/l$, where l

is the pathlength) is computed. It was calibrated to give $c = 0.364$ m^{-1} for clean water. The Q-fluorometer, equipped with a pulsing Xenon flash for excitation, a separate battery pack and a light detector, measures light at the Chl a emission peak. The battery voltage and flash-lamp output were affected by temperature, causing some drift in the output. Therefore, care was taken in comparing slight differences between two casts and in comparing the deep values with the near-surface values. However, fluorometer output was found to be highly correlated with extracted chlorophyll pigments if samples above and below the fluorescence maximum were considered separately. Correlation coefficients as high as 0.98 have been obtained when the fluorometer and water sampling rosette are on the same instrument package. In order to convert fluorescence to chlorophyll, fluorescence was calibrated for each cast separately using the *in vitro* chlorophyll data. Attenuation was converted to SPC using particle counter data for the entire cruise.

BACKGROUND

The beam attenuation coefficient (c) is the sum of the scattering coefficient (b) and the absorption coefficient (a). Furthermore, it can be separated into constant and varying parts. The constant part (c_w) is that due to pure seawater. The varying portion of the dissolved substance is frequently referred to as "yellow matter", since it absorbs strongly in the blue. Dissolved substances do not scatter, so this component is labeled "a_y". The suspended particulate components (SPC) are a_p and b_p. Thus

$$c = c_w + a_y + b_p + a_p.$$

a_y is known to decrease rapidly with increasing wavelength in the visible range. The transmissometer that we use has been designed with a red ($\lambda = 665$ nm) light source, so that the variation is due almost entirely to the suspended particles. Thus we define particulate attenuation

$$c_p(665) = c(665) - c_w(665) = a_p(665) + b_p(665).$$

Particulate absorption and scattering are not independent quantities. Absorption per unit pigment is to some extent dependent on the size, structure and index of refraction of the particle in which it is contained. Nevertheless, pigment content and absorption are highly correlated. Scattering, on the other hand, can be strongly modified by the absorption properties of the particle. In the case where the index of refraction of the particle is close to that of water, an increase in absorption can (for some sizes of particles) result in an even larger decrease in scattering (anomalous diffraction) so that the attenuation actually decreases with an increase in absorption (VAN DE HULST, 1957). Another effect that produces the same result is that the index of refraction is reduced on the short wavelength edge of an absorption band (anomalous dispersion, MUELLER, 1974). The net result for populations of particles found in the ocean is that the beam attenuation coefficient at 665 nm is not very sensitive to the pigment content of the particles (KITCHEN et al., 1983).

The beam attenuation coefficient (c) should not be confused with the diffuse attenuation coefficient (k) which is obtained from measurements of sunlight irradiance penetration in the ocean.

$$k = -d(\ln(E))/dz.$$

Since the irradiance meter detects not only the directly transmitted light but also much of the scattered light, the diffuse attenuation coefficient is much closer to the absorption coefficient than to the beam attenuation coefficient. Thus profiles of k are very similar to profiles of pigment concentration.

Beam attenuation often has been used as a measure of suspended particulate volume or mass concentration (SPINRAD et al., 1983; McCAVE, 1983; BAKER et al., 1983). This is only valid if the size and index of refraction distributions of the particles are relatively uniform from sample to sample. In the central gyre during the ODEX cruise, we observed changes in the size distribution with depth that could have increased the attenuation : volume ratios by more than 60%. The increases actually observed were <40% (KITCHEN et al., 1983).

RESULTS

Distributions of temperature and sigma-T along 155°W

Isopleths of temperature and sigma-t show a general shoaling from 23°N to 40°N latitudes (Fig. 1a). According to REID (1965) the isopleths also shoal toward the south starting from about 15°N so that the isopleths form a cross-section of a bowl. Despite the gap of data between 15°N and 23°N, the pattern shown in Figs 1 and 2 is consistent with the patterns observed by REID (1965) and HAYWARD and McGOWAN (1985), including a hump in the isopleths near 25°N. Continuous horizontal gradients were found for both temperature and salinity in the upper 100 m to the south of 44°N. The isopycnals sloped less than the isotherms since both temperature and salinity increased toward the south. Larger horizontal sigma-t gradients in the surface water were found south of 35°N latitude, the region of subtropical fronts (RODEN, 1981). The low horizontal gradients indicate the subarctic region north of 44°N. The boundary shows relatively small density gradients due to mean balance between temperature and salinity gradients, but it is identified by large temperature and salinity gradients, earning the name Subarctic Front (RODEN, 1975, 1977).

Between 12°N and 15°N, isotherms and isopycnals shoaled sharply toward the equator (Fig. 2) (REID, 1965). The meridional changes in the vertical distributions clearly mark the boundary of the gyre. The patterns across the equator show features of equatorial upwelling in the upper 100 m, downward warm advection below 100 m, and two ridges in isotherms below 100 m located at about 2° latitude in both hemispheres (Fig. 2b). The equatorial upwelling in the upper 100 m is characterized by low temperatures. The ridges also are characterized by low temperatures, suggesting their ties with deeper water. This inference of upwelling is supported by distributions of dissolved oxygen and nutrients (FEELY et al., 1987).

Meridional variations

Fluorescence increased with depth, typically with the peak exceeding by a factor of 3–5 the values in the surface mixed layer (SML) (Figs 3 and 4). The fluorescence maximum is a dominating feature of all the fluorescence profiles, and little ambiguity results from defining its depth coincident with the maximum value. More than one peak may be present, but such occurrences were rare. The secondary peak may be a temporary or transient feature. The peak was ubiquitous but with variable depth and amplitude. In the gyre the depth of maximum fluorescence varied between 75 and 150 m or from 20 to
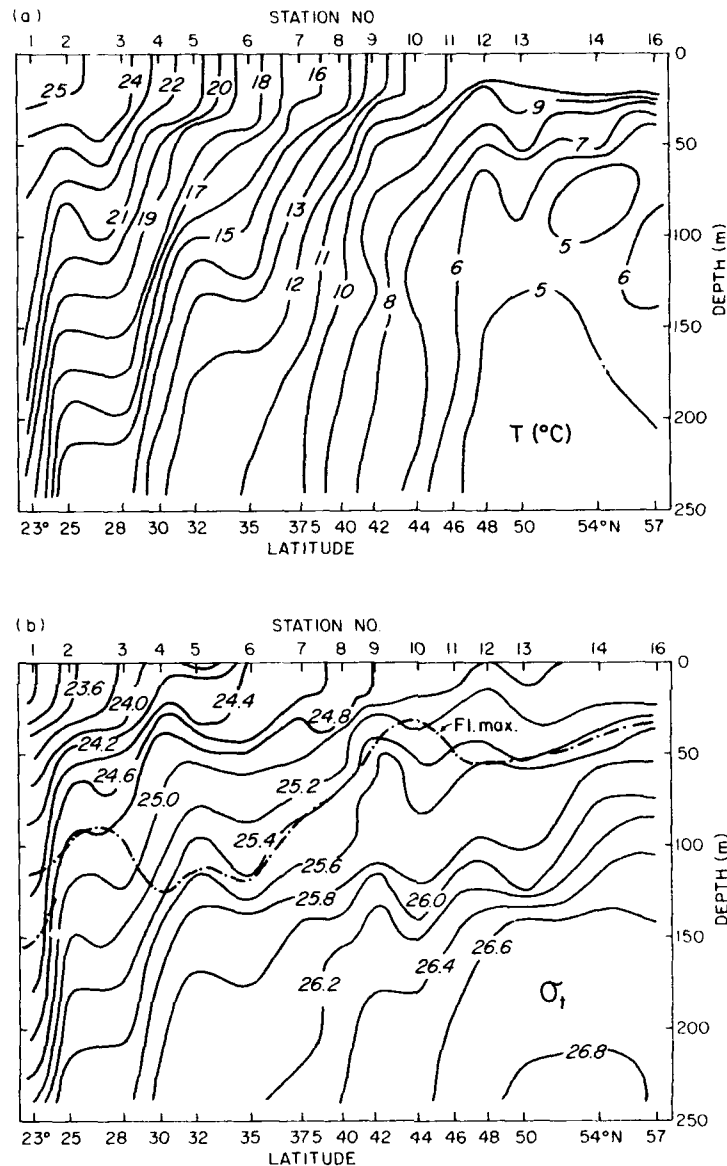
Fig. 1. Distribution of (a) temperature and (b) sigma-*t* along 155°W between 23°N and 57°N as observed on R.V. *Discoverer* during 28 June–23 July 1985. The dash–dot curve indicates fluorescence maximum depths.

70 m greater than the depth of the SML. The depth increased toward the south from the Subarctic Front, reaching the maximum at about 23°N, and decreased from 15°N to 10°N (Figs 3a and 4a). The fluorescence maximum is seen to have the cross-section of a bowl in the region of the central gyre. A similar pattern was shown by VENRICK *et al.* (1973) and SCHULENBERGER (1978). In the central gyre, away from the boundaries, fluorescence was low and showed little meridional gradient in the upper 50 m (Fig. 3a).
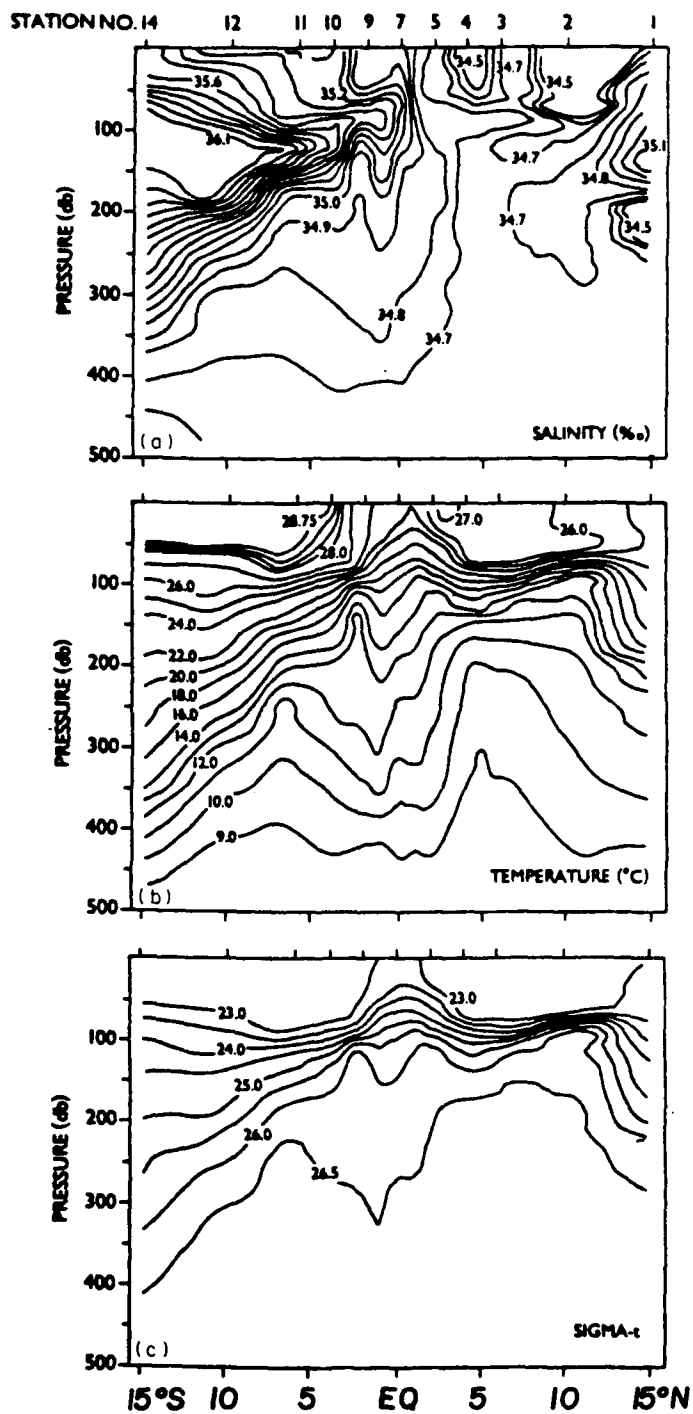
Fig. 2.   Distribution of (a) salinity, (b) temperature, and (c) sigma-*t* along 150°W between 15°N
and 15°S observed on R.V. *Discoverer* during 27 February–9 March 1984.
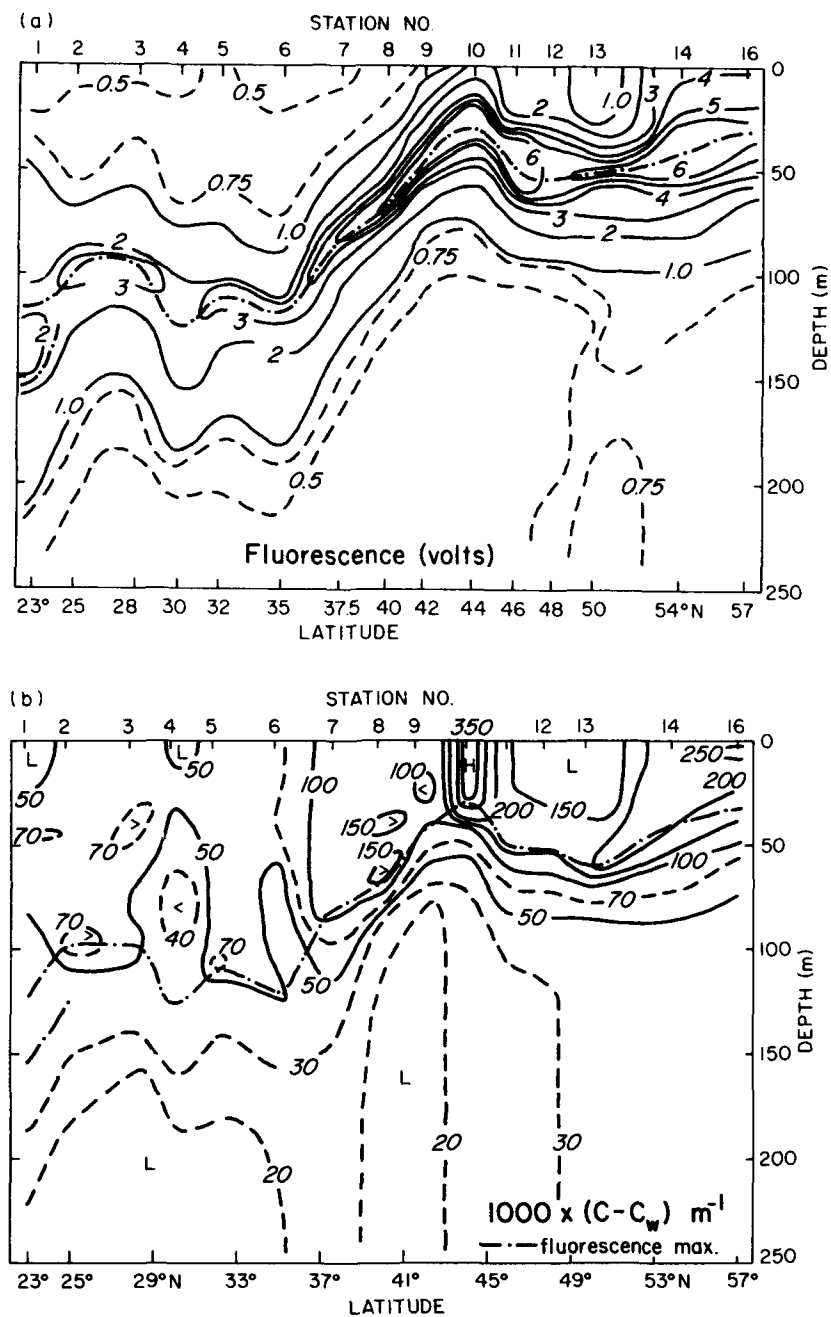
Fig. 3. Distribution of (a) *in situ* fluorescence (in the electrical unit) and (b) beam attenuation coefficient at 665 nm along 155°W between 23°N and 57°N. The dash–dot curve indicates fluorescence maximum depths.
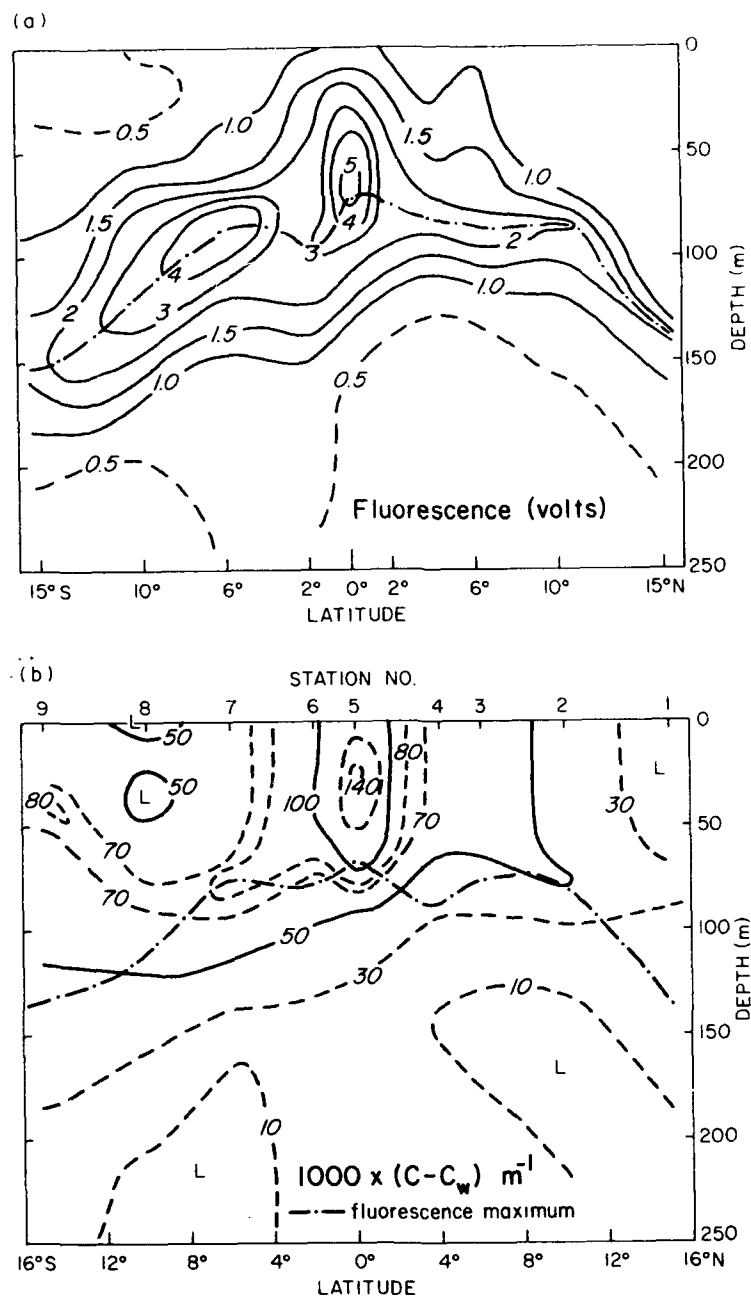
(a)

(b)

Fig. 4. Distribution of (a) *in situ* fluorescence, and (b) beam attenuation coefficient at 665 nm along 155°W between 15°N and 15°S. The dash–dot curve indicates the fluorescence maximum depths.

Fluorescence in the surface water was maximum at the Subarctic Front near 44°N (Fig. 3a). The fluorescence and SPC peaks were shallowest and most intense at this front indicating increased productivity, consistent with the high nutrient concentrations (Fig. 6). The conditions over the equatorial regions were similar to those in the subarctic frontal zone. Over the southern edge of the northern gyre, the fluorescence peak shoaled
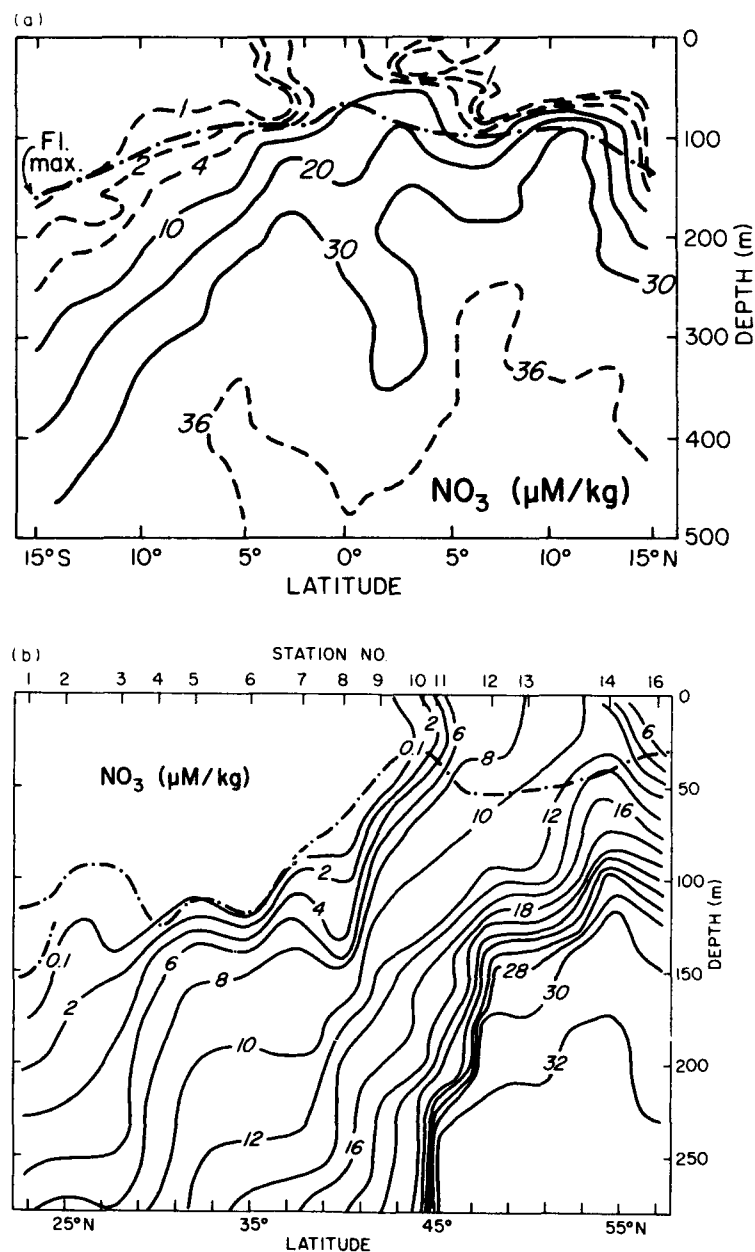

Fig. 5. Distribution of nitrate (a) along 155°W between 23°N and 57°N, and (b) along 150°W between 15°N and 15°S.

and intensified approaching the equator (Fig. 4a); the particulate attenuation increased, and its peak shoaled (Fig. 4b). Nutrient concentrations were elevated near the equator (FEELY *et al.*, 1987).

Nutrients were severely depleted down to the deep fluorescence maximum in the central gyre. The top of the nutricline was at the fluorescence maximum (Fig. 5), as reported by KIEFER *et al.* (1976) and HAYWARD and McGOWAN (1985). Similar conditions were observed by measurements of nutrients at more than 100 stations near 33°N, 142°W during 3 weeks in November 1982 (ODEX-3 cruise). On the other hand, nutrients were present in the surface layer of the subarctic and equatorial regions (Fig. 5), and when nutrients were available in the euphotic zone, biomass (both SPC and chlorophyll) concentrations were higher and the depth of the chlorophyll maximum depth was shallower. The biomass and chlorophyll maxima tended to merge as they shoaled. The distribution of low nitrate water (Fig. 5) closely corresponded to the bowl defined by the fluorescence maximum layer.

DISCUSSION

Theory for interpretation of patterns

We propose that the patterns observed in the north central Pacific can be best explained in terms of the present knowledge of the growth and metabolic regulation of phytoplankton. Specifically, the patterns appear to be determined primarily by the changes in the growth rate and intracellular concentrations of photosynthetic pigments in response to variations in light and nutrients. Although this model (Fig. 6) is a simplification and in particular does not include compartments for detrital and dissolved materials, it is nonetheless useful.

According to this conceptual model, nitrogen is the most limiting element to the growth rate and size of the phytoplankton crop. As such, its availability as dissolved ammonium, nitrite, nitrate or urea is an important determinant of variability in both the concentration of microparticles and the optical properties of these microparticles. The three compartments of this description consist of the total pool of nitrogenous nutrients, the stock of particulate organic (or cellular) nitrogen, and the total amount of Chl *a* found within the stock of particulate organic nitrogen.
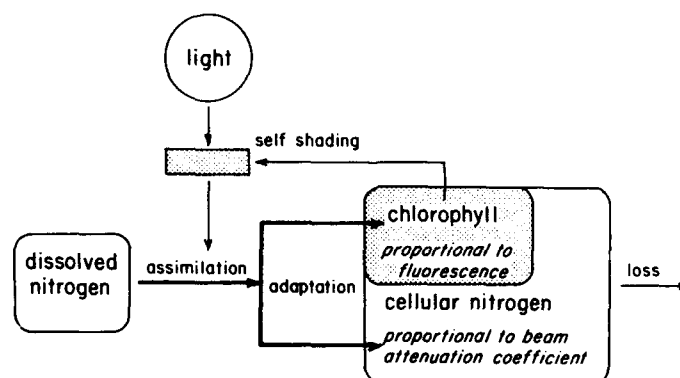

Fig. 6. Diagram of the bio-optical model of nitrogen flux.

Chlorophyll concentrations were obtained from *in situ* fluorescence which we calibrated with measurements obtained from bottle samples. We obtained a separate calibration for each station and often found it necessary to use different relationships above and below the fluorescence maximum. Likewise, the value of the beam attenuation coefficient for particles, $c_p(665)$, is assumed to be proportional to concentration of particulate organic nitrogen (PON) and independent of chlorophyll concentration. The best data we have for comparing chlorophyll, PON, SPC and beam attenuation were collected on the Oregon shelf during a series of monthly cruises spanning 18 months (SMALL *et al.*, 1988). SPC, $c(665)$, (POC), and PON were found to covary in the euphotic zone even in the nearshore regions ($0.76 < r < 0.87$ for all pairs). For the same data set, chlorophyll was much less correlated with any of the others ($0.44 < r < 0.64$). For the present study, we converted beam attenuation to SPC using the particle counter data obtained for the bottle samples. Figure 7 shows the two regressions used and the scatter of data. We expect that most of the scatter is due to random error in the particle counter data. The change in slope of the regression is due to changes in size distribution with depth (KITCHEN *et al.*, 1983).

The rate of conversion of nitrogenous nutrients into cellular nitrogen depends not only upon the ambient concentration of nutrients but also the flux of visible light. As shown in Fig. 6, the assimilation of nitrogen by the crop of phytoplankton can be divided usefully into two flows, one into Chl *a* and other pigments of the chloroplast and the other into all
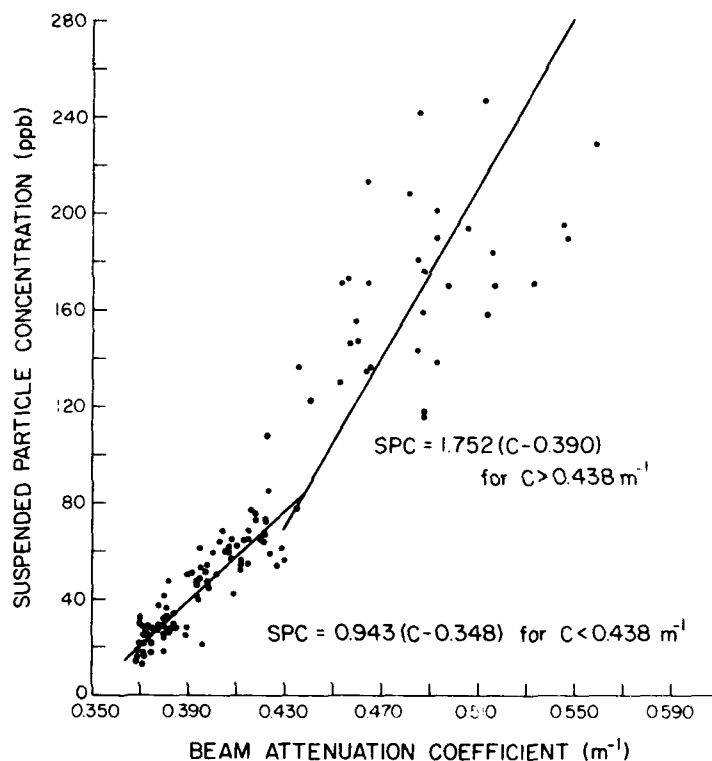

Fig. 7. Particle volume concentration vs beam attenuation coefficient between 23°N and 57°N observed on R.V. *Discoverer* during 28 June–23 July 1985.

other cellular compounds. This process has been labeled "adaptation" since it is now well established that the flow into pigments and nonabsorbing compounds is tightly regulated and varies greatly with conditions of growth. For example, Laws and Bannister (1980) have shown that in the marine diatom, *Thalassiosira weissflogii*, the intracellular concentration of Chl *a* can vary 10-fold depending upon the light intensity and rate of nutrient supply at which they are grown. Cells growing rapidly at high light levels have lower concentrations of pigments than cells growing slowly at lower light levels. On the other hand, cells growing more rapidly because of sufficient supply of nutrients have higher cellular concentrations of pigments than cells growing slowly because of n' trient limitation. In this model the growth rate of the cells is determined by either light intensity or nutrient availability, whichever is more limiting to growth.

Not only does the process of light adaptation lead to predictable changes in the ratio of cellular chlorophyll to carbon, but also the response is similar for species from different classes of algae (Fig. 8). Similarly, dramatic and predictable responses or adaptations to nutrient limitation have been found (Cullen, 1982). Since light limitation leads to increases in cellular pigments and nutrient limitation leads to decreases in cellular pigments, cells whose growth is light-limited will always have higher cellular concentrations of chlorophyll than those whose growth is limited by nutrients.

The concentration of Chl *a* (or more precisely the concentration of pigments of the phytoplankton crop) is the principal source of variability in the attenuation of visible sunlight (e.g. Riley, 1956) (Fig. 6). According to our model (see also Kiefer, 1984, 1986), there are two causes of variability in pigment concentration in the sea: those caused by changes in the concentrations of particles that contain these pigments, and those caused by changes in the concentration of pigments within these particles.

The concentration of particles or cellular nitrogen within the water column will depend upon all the ecological factors that determine the rates of production and loss cf microparticles. While these factors are not well understood, it is reasonable to assume
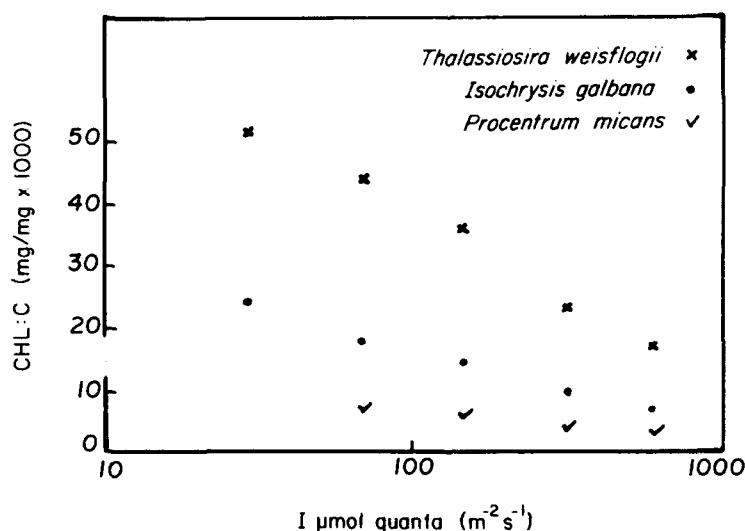

Fig. 8. Chlorophyll/carbon ratios as a function of light level for three cultures of phytoplankton grown at constant nutrient levels. Data from Falkowski *et al.* (1985).

that within a lighted and stratified water column, the concentration or rate of supply of nitrogenous nutrients is most important, determining the upper limit to the stock of PON. On the other hand regulation of the cellular concentration of pigment is a physiological process that depends principally upon only light intensity and nutrient availability. Figure 6 indicates that variations in cellular nitrogen will cause proportional changes in the beam attenuation coefficient, and variations in the concentration of chlorophyll within the cell will cause variations in the ratio of Chl a fluorescence to the beam attenuation coefficient.

KIEFER and KREMER (1981) have formulated a mathematical description of growth and cellular chlorophyll concentration by the phytoplankton crop. The cellular concentration of chlorophyll, Chl/PON, at depth is described simply in terms of two variables, the gross specific growth rate of the crop, $\mu + r$, and the scalar irradiance, E_0, and two constants, the quantum yield of nitrogenous nutrient uptake, $\phi(N)$, and the chlorophyll specific absorption coefficient a_p^*:

$$\text{Chl/PON} = (\mu + r)/E_0 a_p^* \phi(N), \ 0.2 < \text{Chl/PON} < 2.3. \tag{1}$$

r is the specific rate of respiration and μ is the specific rate of net growth. Chl/PON varies only between set limits. This formulation provides a quantitative description of increases in cellular chlorophyll with increases in nutrient availability (affected by increases in $\mu + r$), and increases in cellular chlorophyll with decreases in light intensity (affected by decreases in E_0 that exceed decreases in $\mu + r$). The formulation also can be used to calculate the light level and growth rate at which cellular pigment concentration is maximal.

The predicted profiles of Chl/PON for the central gyre and for a typical subarctic station are shown in Fig. 9. EPPLEY et al. (1973) report a growth rate of 0.22 doublings per day down to 90 m in the central gyre. This is equivalent to a specific growth rate of 0.15 day^{-1}. Below 90 m the growth rate drops rapidly. To obtain quanta of light, we numerically integrated our irradiance spectra (Sta. 3) obtained near noon and then divided it by 4 to estimate an average for an entire 24 h. Values of a^* and $\phi(N)$ were taken from KIEFER and KREMER (1981). The minimum value of Chl/PON was not surpassed until 40 m depth, and the maximum value was attained at 95 m (1.5% of surface irradiance). For the subarctic case, we used a growth rate of 0.30 day^{-1} (SUPER, 1987) which was a vertically integrated average. Light data were taken from Sta. 9. The minimum Chl/PON was surpassed at 5 m and the maximum obtained at 40 m (~5% surface irradiance).

Observed profiles for the two stations are given in Fig. 10. The exponential increase with depth of Chl/SPC is quite evident, and the depths of the maxima are close to those predicted. The Chl/SPC maximum is maintained at relatively constant value for roughly 10 m and then decreases again. Pigment bleaching in extremely low light levels has been reported for laboratory cultures by FALKOWSKI (1980), so this is not unexpected. Of note is the fact that the particle and chlorophyll maxima coincide at Sta. 9. Coincidence and lack of coincidence of the particle and chlorophyll maxima do not necessarily indicate a differing mechanism for the formation of the chlorophyll maximum. The ratio of Chl/SPC increases rapidly between the surface and the depth of the coincident maxima (Fig. 10b). This behavior also has been observed in productive coastal upwelling regions where the maxima are as shallow as 20 m (SMALL et al., 1988).
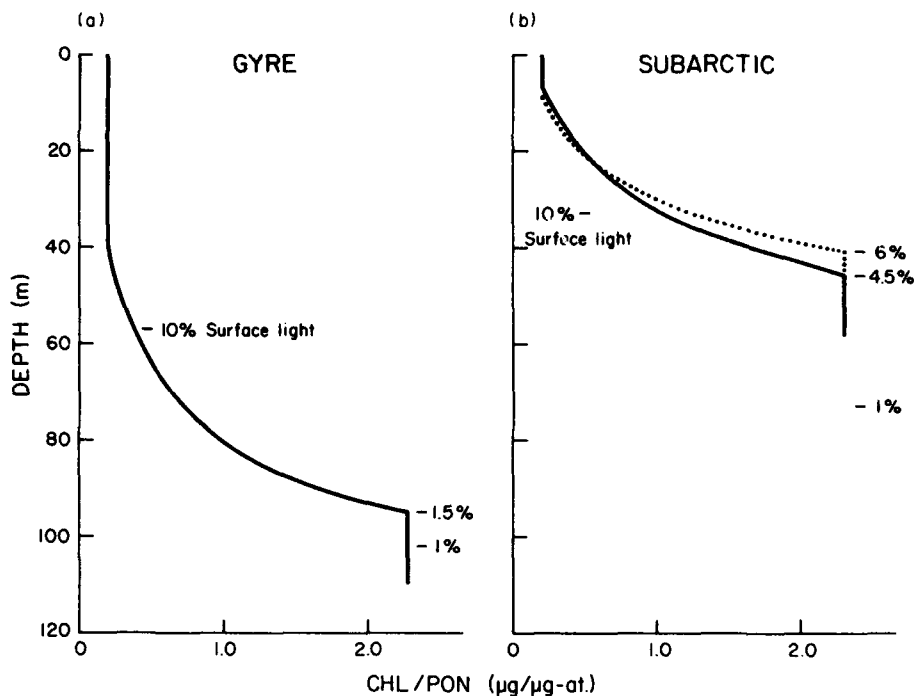
Fig. 9. Profiles of Chl/PON predicted by equation (1) and observed irradiance profiles for (a) central gyre ($\mu = 0.15$ day^{-1}) and (b) subarctic region ($\mu = 0.30$ day^{-1}) and --- ($\mu = 0.2$ day^{-1} + 0.005 × depth).

Spatial variation in particle concentration

The vertical distribution of $c_p(665)$ generally can be characterized as two-layered. The waters above the chlorophyll maximum contain high concentrations of particles with little vertical change. Below the chlorophyll maximum concentrations decrease rapidly with depth (Figs 3b and 4b). In keeping with the model in Fig. 6, it appears that the boundary of the two layers is determined by the penetration of sunlight, the boundary being at or near the bottom of the euphotic zone.

Since attenuation at the longwave end of the spectrum is large, the percent penetration of 488 nm at a given depth is always larger than that of the total sunlight (Fig. 11). However, beneath the top several meters, most of the light is in the blue-green region, so the 488 nm values give a valid approximation of the meridional variation of the total sunlight penetration. Notice the sunlight penetration changes along the fluorescence maximum layer, from less than 1% in the gyre to more than 10% in the transition zones.

At some stations this simple pattern in vertical distribution was complicated by the presence of a subsurface particle maximum. Within the gyre the surface particle maximum is weak and occurs above the chlorophyll maximum and near the bottom of the mixed layer. Within the latitude of equatorial upwelling the particle maximum is more strongly developed and found near the bottom of the mixed layer at a depth close to that of the chlorophyll maximum. In the subarctic the particle maximum is again strong and found at or near the chlorophyll maximum.
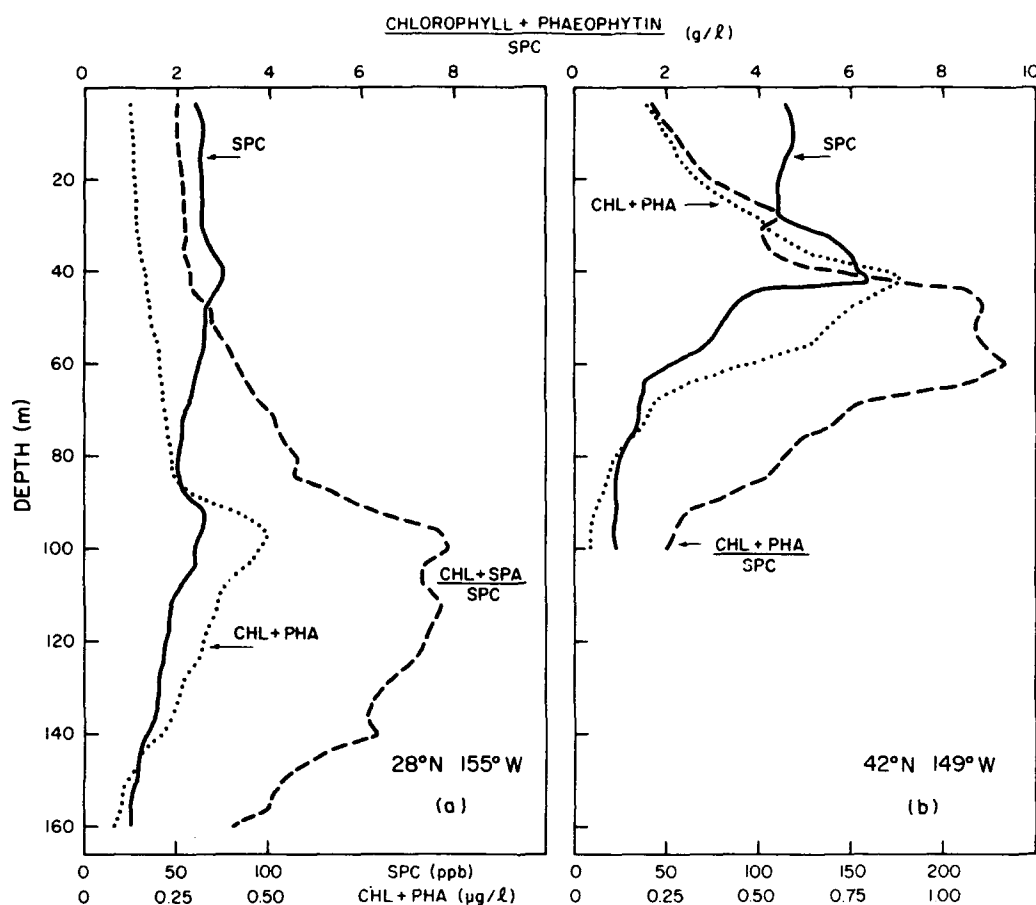
Fig. 10. Observed profiles of chlorophyll + phaeophytin, suspended particle concentration and (Chl + PHA)/SPC for stations at (a) 28°N 155°W and (b) 42°N 149°N.

While the vertical distribution of $c_p(665)$ or particles is determined by light, their meridional change appears to be at least loosely determined by nutrient concentration. Inspection of Figs 3b and 4b shows that at the equator the highest value of $c_p(665)$ was 0.14 m^{-1}, the coefficient dropped to a minimum of 0.05 m^{-1} in the gyre, and it rose again to values above 0.2 m^{-1} in the subarctic. A comparison of Fig. 3b with Fig. 5 indicates that in the tropical and temperate Pacific (here 15°S to 40°N) the concentration of microparticles in surface waters increases as the isopleths for nitrate shallow. The shallowing of isopleths for nitrate is also accompanied by increases in the density of surface water and thus decreases in the stratification of the water column. Both the shallowing and the decrease in stability due to decreased stratification are consistent with increase in availability of nutrients within the euphotic zone.

North of 40°N nitrate concentrations were high in surface water, and as would be expected, particle concentrations are high. Variations in $c_p(665)$ within the subarctic do not show a clear meridional trend corresponding to a lack of such a trend in nitrate.
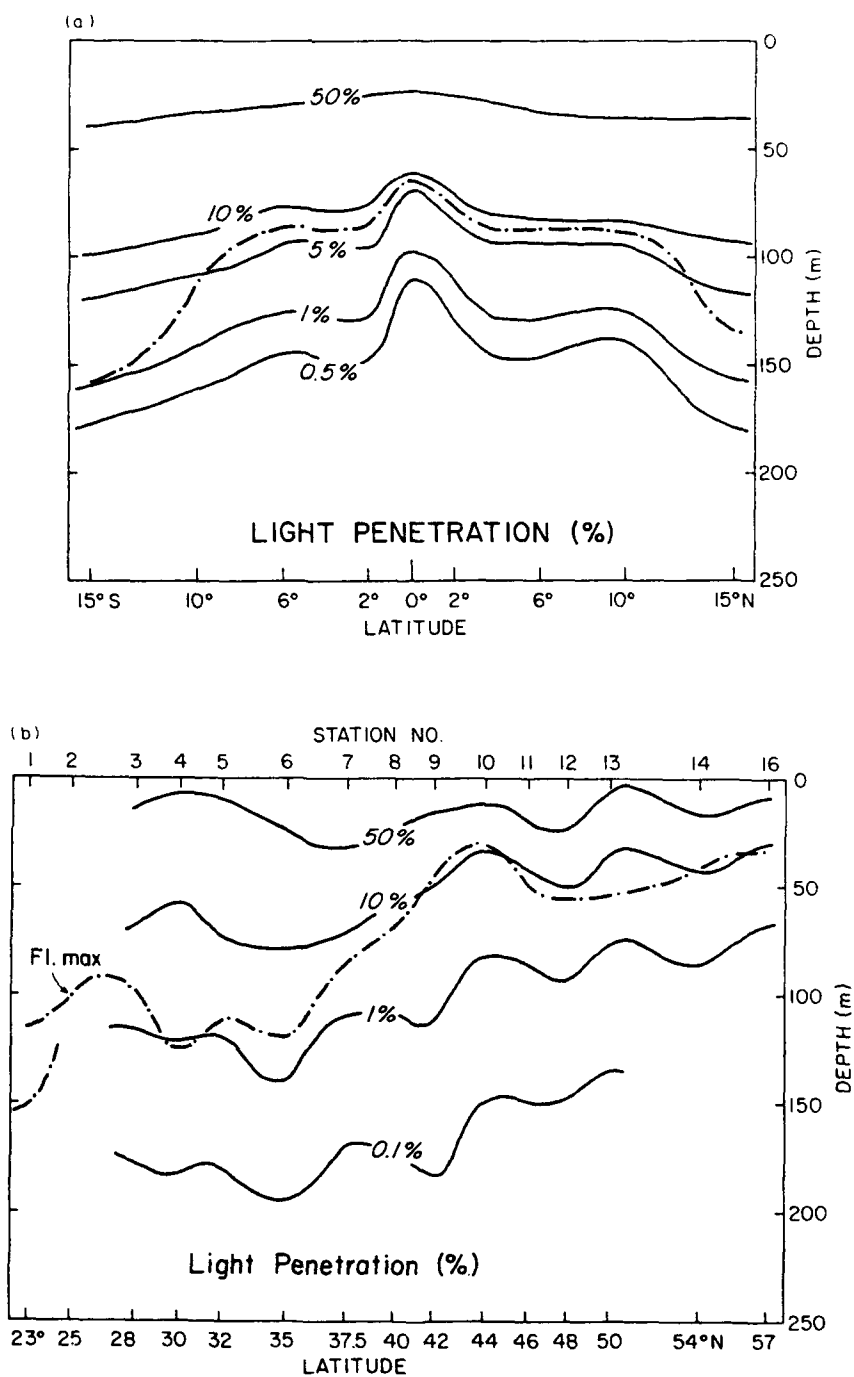
Fig. 11. Sunlight penetration as fractions of the incident light: (a) between 15°N and 15°S along
150°W, and (b) between 23°N and 57°N along 155°W.

Spatial variation in chlorophyll content per particle

If the concentration of chlorophyll within the microparticles remains constant, patterns in the distribution and chlorophyll would be similar to those of $c_p(665)$. However, the patterns are different (Fig. 3a and b), indicating that more chlorophyll does not represent more particles and vice versa. According to the model concept, this non-parallelism is explained largely by adaptation of phytoplankton to the light intensities and nutrient concentration at depth. Such adaptation results in predictable changes with depth in the ratio of chlorophyll to particle concentration.

The simple trend of increases in the ratio of chlorophyll to SPC with depth down to its maximum is seen at all latitudes (Fig. 12). These features or details of this general pattern of increasing pigment concentration per particle are noteworthy and consistent with the concept of equation (1).

Above all, the variations of the pigment per particle in the water column can be large. For example, in the center of the North Pacific gyre, the ratio varies by over 5-fold from its minimum value in the mixed layer to its maximum value at the depth of the chlorophyll maximum. These variations in the ratio of chlorophyll fluorescence to SPC are well within the range of changes in the ratio of cellular chlorophyll to nitrogen measured for cultures of phytoplankton.

Additionally, the changes with depth are best described by three layers. Near the surface mixed layer the ratio is low and changes little with depth. This is to be expected since the phytoplankton in the mixed layer are growing in high light conditions, and the chlorophyll content will be minimal. Above the chlorophyll maximum, the ratio increases rapidly with depth. The crop of phytoplankton adapts to decreasing light levels by increasing its capacity to absorb light. There is of course an upper limit to the cellular concentration of chlorophyll, and this upper limit is reached near the depth of the chlorophyll maximum. The second layer is thus defined. Below the chlorophyll maximum the ratio is high but decreases slowly with depth. Within this layer photosynthetic growth, particle concentrations and pigment concentrations decrease rapidly with depth, and local remineralization is the dominant process.

Chlorophyll maximum

Several hypotheses have been presented to describe the development and maintenance of the deep chlorophyll maximum layer. Recently, VENRICK (1982) presented arguments against the hypotheses of (1) accumulation of cells at a density discontinuity due to decrease in sinking (RILEY et al., 1949; STEELE and YENTSCH, 1960) or behavior of phytoplankton such as vertical migration and aggregation (CULLEN, 1982), and (2) differential grazing pressure (LORENZEN, 1967). The first hypothesis was challenged by the absence of necessary density discontinuity (VENRICK, 1982), by the absence of biomass maximum (BEERS et al., 1975; KIEFER et al., 1976), and by the abrupt change in the species composition across the layer (VENRICK, 1982). The second hypothesis was also disproved by the vertical change in species composition unless grazing is species specific and grazers are distributed in two layers like phytoplankton.

A third hypothesis is that the pigment maximum is due to the physiological adaptation of the cells to the light conditions, and thus is consistent with our observations and model. We will conclude our discussion with a more detailed examination of this hypothesis.
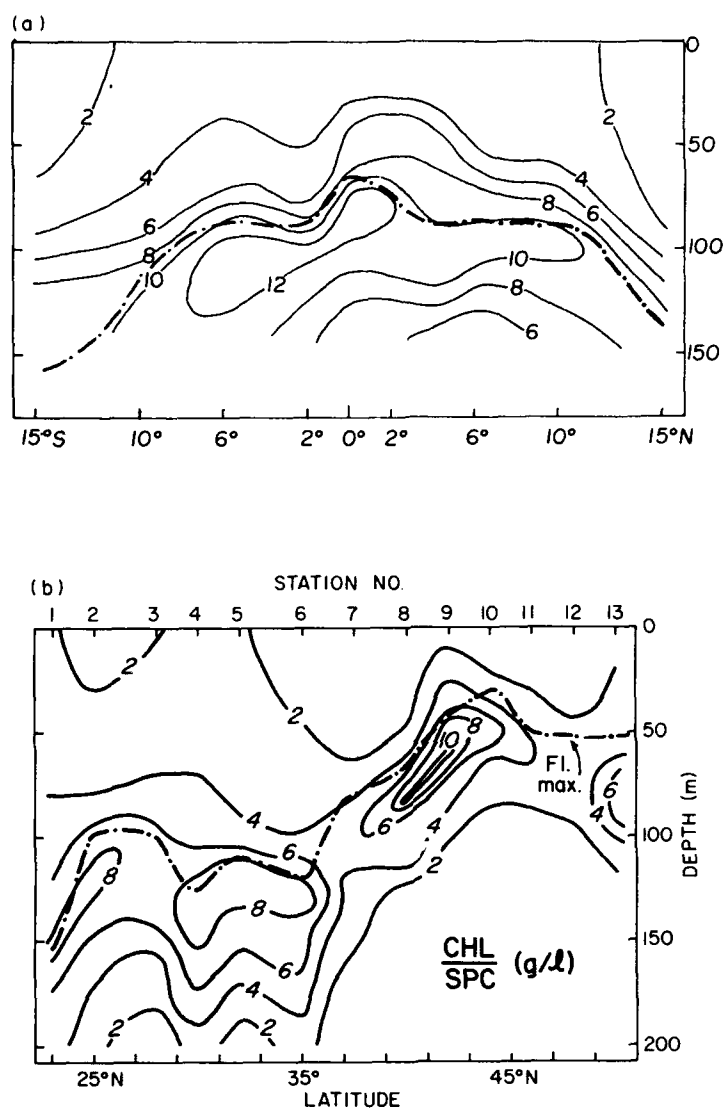
(a)

(b)

STATION NO.

Fig. 12.   Meridional transect of Chl : SPC ratios (a) between 15°N and 15°S along 150°N and (b)
between 23°N and 50°N along 155°W.

An examination of Figs 3a and 4b indicates that the chlorophyll maximum is both at its
greatest depth and least concentration in the center of the gyre. It shallows rapidly and
intensifies north of 35°N and south of 15°N. The model predicts such a general pattern,
and it also suggests that light adaptation can vary according to nutrient availability.

In the gyre where nutrient concentrations were below our limits of detection, the depth
of the chlorophyll maximum tracks fairly well the depth of the 1 μM nitrate isopleth. It
also tracks the depth of the 1% light level. This correspondence is consistent with earlier
statements that the chlorophyll maximum occurs at the depth where the cellular
concentration of chlorophyll is maximal and is caused by an adaptation to low light level.

In the nutrient-impoverised gyre this will occur at considerable depth because the contribution by shelf-shading to diffuse attenuation of irradiance is small. The nutrient limitation within the upper water column will also depress growth rates, and thus the cellular concentration of chlorophyll will be further reduced (equation 1). The light level at which the cellular concentration of chlorophyll is maximal is close to 1% of incident irradiance, and thus the chlorophyll maximum is expected to be near the bottom of the euphotic zone. Below the depth at which Chl/PON attains its maximum, the cells will be unable to absorb enough light to assimilate all the available nutrients. Thus, the chlorophyll maximum is expected to track the top of the nutricline.

At the northern and southern boundaries of the gyre, where the availability of nitrate to the crop increases, the chlorophyll maximum shallows and the tracking by the chlorophyll maximum of the 1% isolume and the isopleth for 1 μm nitrate fails. The chlorophyll maximum rises to almost the 10% isolume and appears to break free of a close correspondence with latitudinal changes in nitrate.

The shallowing of the chlorophyll maximum is the result of the increased attenuation of light with depth, an effect of self-shading. This is the expected result of increased nutrient concentrations and thus increased growth rate, resulting in more particles and higher chlorophyll content. The more rapid increase in Chl/SPC with depth at the equator and in the subarctic region is, in turn, caused by the more rapid decrease in light levels. Also, the absence of nutrient limitation is expected to cause increases in the ratio.

The shallowing of the chlorophyll maximum at the northern and southern margins of the gyre to depths of increasing light intensity also can be explained. As long as growth is not light-limited, the cell chlorophyll content will follow equation (1), increasing with depth until further increases are physiologically impossible. At this point growth becomes light-limited in which the growth rate decreases exponentially with depth, and the chlorophyll content stays constant or decreases slightly with depth. If the growth rate (in the non light-limited case) is higher, equation (1) predicts that the maximum chlorophyll content will be obtained at a higher light level. We have observed this in the equatorial and subarctic regions. CULLEN and EPPLEY (1981) observed similar circumstances in coastal waters off the Southern California bight.

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